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Invasion and expansion of cooperators in lattice populations: Prisoner's dilemma vs. snowdrift games

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ABSTRACT

The evolution of cooperation is an enduring conundrum in biology and the social sciences. Two social dilemmas, the prisoner's dilemma and the snowdrift game have emerged as the most promising mathematical metaphors to study cooperation. Spatial structure with limited local interactions has long been identified as a potent promoter of cooperation in the prisoner's dilemma but in the spatial snowdrift game, space may actually enhance or inhibit cooperation. Here we investigate and link the microscopic interaction between individuals to the characteristics of the emerging macroscopic patterns generated by the spatial invasion process of cooperators in a world of defectors. In our simulations, individuals are located on a square lattice with Moore neighborhood and update their strategies by probabilistically imitating the strategies of better performing neighbors. Under sufficiently benign conditions, cooperators can survive in both games. After rapid local equilibration, cooperators expand quadratically until global saturation is reached. Under favorable conditions, cooperators expand as a large contiguous cluster in both games with minor differences concerning the shape of embedded defectors. Under less favorable conditions, however, distinct differences arise. In the prisoner's dilemma, cooperators break up into isolated, compact clusters. The compact clustering reduces exploitation and leads to positive assortment, such that cooperators interact more frequently with other cooperators than with defectors. In contrast, in the snowdrift game, cooperators form small, dendritic clusters, which results in negative assortment and cooperators interact more frequently with defectors than with other cooperators. In order to characterize and quantify the emerging spatial patterns, we introduce a measure for the cluster shape and demonstrate that the macroscopic patterns can be used to determine the characteristics of the underlying microscopic interactions.

1. Introduction

The evolution of cooperation poses a fundamental challenge to evolutionary biologists (Axelrod, 1984; Maynard Smith, 1982; Nowak, 2006). Cooperators incur costs in order to benefit others while defectors reap the benefits but dodge the costs. Despite the fact that groups of defectors perform poorly as compared to groups of cooperators, Darwinian selection should favor defectors. Nevertheless, cooperation is ubiquitous in biological and social systems. The problem of cooperation represents a social dilemma characterized by the conflict of interest between the group and the individual (Dawes, 1980; Hauert, 2006).

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The two most prominent mathematical metaphors to investigate cooperation in social dilemmas are the prisoner's dilemma and the snowdrift game (Doebeli and Hauert, 2005). Both games describe pairwise interactions where each player can cooperate or defect. In the prisoner's dilemma, a cooperator incurs a cost, c, and provides a benefit, b, to its opponent with $b > c$. Defectors neither incur costs nor provide benefits. Hence, if both players cooperate, each receives $b-c$ but neither gains anything if they both defect. If a cooperator meets a defector, the defector gets the benefit and the cooperator is left with the costs. The different outcomes can be conveniently summarized in a payoff matrix:

$$\begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix}. \qquad (1)$$

It is easy to see that defection is dominant, i.e., it is better to defect, irrespective of the other player's decision. Consequently, the two players end up with zero instead of the more favorable reward $b-c$ for mutual cooperation. Self-interest prevents individuals from achieving a mutually beneficial goal, which is the essence of social dilemmas.

In the snowdrift game individuals can gain access to benefits for the pair at some individual cost. Cooperators are willing to bear the costs whereas defectors are not. If two cooperators meet, both get the benefit and share the costs, $b-c/2$, and if a cooperator meets a defector, the cooperator still gets the benefit but carries the entire costs, $b-c$. For the defector, the payoffs are the same as in the prisoner's dilemma. The resulting payoff matrix is

$$\begin{pmatrix} b-\frac{c}{2} & b-c \\ b & 0 \end{pmatrix}. \tag{2}$$

The crucial difference is that the best decision now depends on the other individual: defect if the other player cooperates but cooperate if the other defects. This results in a relaxed social dilemma—cooperation remains prone to exploitation by defectors but at least they receive their share of the benefit.

The replicator dynamics (Hofbauer and Sigmund, 1998) is used to describe the evolutionary fate of cooperators and defectors in large, unstructured populations where each individual is equally likely to interact with any other one. In the prisoner's dilemma cooperation disappears and a pure defector population is the only stable outcome. In contrast, in the snowdrift game cooperators and defectors can co-exist at an equilibrium frequency of $1-c/(2b-c)$ cooperators. The fact that in the snowdrift game it is best to adopt a strategy that is different from the opponent ensures that in a population the rare type is favored and guarantees stable co-existence. Also note that the average payoff in equilibrium is lower than for a population of cooperators—another consequence of social dilemmas (Doebeli and Hauert, 2005).

In such well-mixed populations the invasion and maintenance of cooperation is trivial in the snowdrift game but additional supporting mechanisms are required for cooperation to succeed in the prisoner's dilemma. Over the last decades, much theoretical effort has been expended in order to identify different means to support cooperators (Hamilton, 1964; Hauert et al., 2002, 2007; Imhof and Nowak, 2010; Nowak and Sigmund, 1998; Trivers, 1971). One surprisingly simple way to achieve this goal is to include spatial dimensions and to consider spatial games where individuals are arranged on a lattice and their fitness is based on interactions within their local neighborhood (Hauert, 2001, 2002; Nakamaru et al., 1997, 1998; Nowak and May, 1992, 1993; Nowak et al., 2010; Ohtsuki et al., 2006; Ohtsuki and Nowak, 2008; Pacheco et al., 2006; Szabó and Tőke, 1998; Tarnita et al., 2009a, b; Taylor et al., 2007). This enables cooperators to form clusters and thereby reduces exploitation by defectors. The spatial dynamics of the prisoner's dilemma has attracted increasing interest from different disciplines (for an excellent review see Szabó and Fáth, 2007).

Naturally, it is of particular importance to understand how initially rare cooperators can increase and get established in a population. According to the replicator dynamics, this never happens for the prisoner's dilemma in infinite populations but due to the inherent stochasticity in finite populations, there exists a small probability that even a single cooperator can invade and eventually take over an entire population (Nowak et al., 2004; Taylor et al., 2004). Although, this chance tends to be exceedingly small and decreases rapidly with increasing population size. However, in spatial populations, even a small patch of cooperators may trigger a successful and persistent invasion of cooperators (Ellner et al., 1998; Langer et al., 2008; Le Galliard et al., 2003; Nakamaru et al., 1997, 1998; Ohtsuki et al., 2006; Taylor et al., 2007; van Baalen and Rand, 1998).

While the invasion of cooperators in the snowdrift game is trivial in well-mixed populations, it turns out that the conditions are less clear in spatial settings because in the spatial snowdrift game the limited local interactions often reduce or even eliminate cooperation (Hauert and Doebeli, 2004). Interestingly, the fact that it is better to adopt a strategy that is different from your opponent promotes cooperation and is responsible for the co-existence of cooperators and defectors in well-mixed populations, but the same mechanism often inhibits cooperation in spatial settings, because it hampers the formation of compact clusters of cooperators. Thus, in well-mixed populations establishing co-operation based on the snowdrift game is easy but unlikely for the prisoner's dilemma, whereas in spatial settings the odds seem to be reversed—space promotes cooperation in the prisoner's dilemma but not necessarily in the snowdrift game. Here we compare and contrast the microscopic and macroscopic features and characteristics of the spatial invasion process governed by these two types of social dilemmas.

2. Model

Consider a spatially extended population where each individual is situated on one site of a two-dimensional $L\times L$ square lattice with periodic boundary conditions. There are no empty sites. All individuals engage in pairwise interactions with each neighbor in their Moore neighborhood, i.e., with the eight nearest neighbors reachable by a chess-kings-move. The payoffs of all interactions are accumulated. The payoff matrices for the prisoner's dilemma and the snowdrift game can be conveniently rescaled such that they depend only on a single parameter (Doebeli and Hauert, 2005; Hauert and Doebeli, 2004; Langer et al., 2008). For the prisoner's dilemma we get

$$\begin{pmatrix} 1 & 0 \\ 1+u & u \end{pmatrix}, \tag{3}$$

where $u=c/b$ denotes the cost to benefit ratio of cooperation and for the snowdrift game

$$\begin{pmatrix} 1 & 1-v \\ 1+v & 0 \end{pmatrix}, \tag{4}$$

where $v=c/(2b-c)$ indicates the cost to net benefit ratio of mutual cooperation. With $b>c$, both u and v are constrained to the interval [0,1]. Note that these parameterizations are very different from the so-called weak prisoner's dilemma, which goes back to Nowak and May (1992) and actually marks the borderline between the prisoner's dilemma and the snowdrift game. However, in spatial settings a clear distinction is of particular importance because space often has the opposite effect on cooperation in the two games (Hauert and Doebeli, 2004).

The population is asynchronously updated by randomly selecting a focal individual x to reassess and update its strategy by comparing its payoff P_x to that of a randomly chosen neighbor y. The focal individual x adopts y's strategy with a probability proportional to the payoff difference, provided that $P_y>P_x$. Specifically, the transition probability $f(P_y-P_x)$ can be written as

$$f(P_y-P_x)=\begin{cases} \frac{P_y-P_x}{\alpha} & \text{if } P_y>P_x, \\ 0 & \text{otherwise,} \end{cases} \tag{5}$$

where α denotes a normalization constant such that $f(P_y-P_x)\in[0,1]$. Here, $\alpha=k(1+u)$ or $\alpha=k(1+v)$, respectively, and $k=8$ represents the number of neighbors.

Note that this update rule, Eq. (5), is semi-deterministic, as individuals never imitate strategies of worse performing